A fish introduction and its impact on the plankton community

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Preface

This study was carried out in the Aquatic Behavioural Ecology (ABE) research group at the University of Bergen, Norway. My supervisors were Petter Larsson (ABE, UiB), Anders Hobæk (Norwegian Institute for Water Research & UiB, Bergen) and Frank Knudsen (SIMRAD Kongsberg Maritime AS, Horten, Norway). During the study period, I was supported by a Quota stipend from the Norwegian State Education Loan Fund (Lånekassen), The L. Meltzer college fund, and my own funding.

The original plan for this study was to investigate the behaviour and life history strategies of the larvae of the phantom midge (*Chaoborus flavicans*) in lakes with and without planktivorous fish. For this Lake Myravatn was selected as the lake without such fish and Lake Borevann in Horten in eastern Norway as the lake where *C. flavicans* lived sympatrically with planktivorous fish. The study would be based on both field studies and laboratory experiments. However, it was recognized in 2008 that perch had been introduced to Lake Myravatn and thus it was no longer possible to study the rare phenomenon of *C. flavicans* as a top predator in the pelagic zone of a mesotrophic lake. The approach and objectives were therefore switched to study the development of the introduced fish and how it affects the zooplankton community in the lake.

Acknowledgements

I would like to thank my supervisors Petter Larsson (UiB, Bergen), Anders Hobæk (NIVA, Bergen) and Frank R. Knudsen (SIMRAD, Horten) for all their help, inspiration, guidance, and supervision during this PhD work. Petter's help during writing was memorable. Anders was always straightforward in practical and lab approaches, even more so in writing. Frank taught me how to operate and handle the acoustic equipments and results. I found him always cooperative and quickly responsive. I am grateful to the Norwegian State Education Loan Fund (Lånekassen) for providing financial support to study at the University of Bergen. I would also like to thank the Aquatic Behavioural Ecology (ABE) research group, The Meltzer fund and the Department of Biology, UiB for providing research-related financial and other supports during this study. Let me also to thank the co-authors of the papers included in this thesis who have helped me during the PhD period.

I am very grateful to Knut Helge Jensen for statistical analysis and Ingrid Wathne for her help in field and lab work. In addition, they helped me in many other practical aspects during this study. I would also like to thank Cathy Jenks for her help in improving my written English.

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I am very grateful to my family members here in Bergen. My son Bipul and daughter Prashamsa have many plans and questions after the PhD. I hope I will have time to share and solve them. My wife Purnima has supported me all the way through my PhD. She has maintained us when my scholarship run out including other ups and downs during the PhD putting her study back and now it's my turn to support her pending study.

Finally I would like to dedicate this work to my parents for their never ending support and inspiration through my life.

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Abstract

This thesis is about how one species can invade an ecosystem and change the whole biological community within a few years. The question is whether such changes can be foreseen or are more or less unpredictable?

Biological communities in lakes are vulnerable to fish predation and the zooplankton is strongly affected by the fish types present. Of particular importance is whether they feed on zooplankton (planktivore), benthic animals (benthivore) or are fish eaters (piscivore).

Lake Myravatn in Bergen had for a long time a very rare fish community consisting of only piscivore fish due to the introduction of Northern pike (*Esox lucius*) about 200 years ago. No other fish survived there except some eel (*Anguilla anguilla*). The consequence of this was a zooplankton community with large species that are usually eliminated by planktivorous fish. Predation on the zooplankton was caused by an invertebrate, larvae of the phantom midge (*Chaoborus flavicans*), feeding on small zooplankton individuals.

This situation was completely changed when Eurasian perch (*Perca fluviatilis*) was illegally introduced by unknown person(s) and for unknown reasons, most likely in autumn 2006. Since studies on the zooplankton were ongoing, the consequences for the zooplankton could be recorded. The monitoring of the lake included both quantitative and qualitative zooplankton sampling and fishing with multi-mesh gill nets and echo-sounding able to discriminate between fish and larvae of phantom midge.

Contemporary theory predicted that the perch would encounter very good conditions in the lake with a superabundance of invertebrate prey of optimal size. Both growth and reproduction would be exceptional and a dense perch population would quickly establish. This would reduce the large zooplankton species in the lake, i.e. *Daphnia pulex, D. longispina* and the phantom midge larvae. Disappearance of the invertebrate predator, the phantom midge, and the competitors, the daphnids,

would give an opportunity for smaller species to flourish. The large zooplankton would try to escape fish predation by undergoing diel vertical migration whereby they hide in the dark at great depths during day time and feed on small zooplankton in the upper water layers only during night.

The predictions were mostly correct. The large zooplankton species more or less disappeared and other species took over. A marked change occurred when the small *Bosmina longirostris* took over as the most abundant species in 2010. Over time, also rotifers increased in number of species. This was supposed to be an indirect response to changes in the invertebrate predation regime. Diel vertical migration started for the phantom midge larvae coincidentally with the appearance of the perch. This reduced the time the phantom midge could feed and it changed its life history to one generation per year while previously it had two generations per year. Although the *Chaoborus* started diel vertical migration, their density became very much reduced, and their predator avoidance behaviour was not sufficient for survival. Possibly, over the 200 years without fish predation, they might have lost their ability to go deep enough to avoid the fish.

It was unexpected that it took such long time to change the zooplankton community in Lake Myravatn in spite of the fast development of the perch population. It took three years before *B. longirostris* appeared, and more changes seem to have occurred after that. The pike in the lake that for long had survived without fish prey, suddenly had a superabundance of new prey when the perch came, but although individual pike increased their growth, a numerical response was not noticeable.

This study showed that contemporary theory concerning food-web structure in lakes is mainly correct. However, it is necessary to better quantify the processes involved to foresee the time it takes to cause changes and for predicting the effects on other parts of the freshwater ecosystem than just zooplankton and fish.

List of papers

Paper I:

Regmi, B. P. & P. Larsson. Development and diet of Eurasian perch (*Perca fluviatilis*) when invading a lake without planktivorous fish (manuscript).

Paper II:

Regmi, B. P., J. S. Wivegh, F. Knudsen & P. Larsson. Vertical distribution and diel migration of phantom midge (*Chaoborus flavicans*) larvae before and after invasion of Eurasian perch (*Perca fluviatilis*). submitted.

Paper III:

Regmi, B. P., J. S. Wivegh & A. Hobæk. Population decline and life-cycle adjustment in a phantom midge (*Chaoborus flavicans*) population after introduction of planktivorous fish (manuscript).

Paper IV:

Regmi, B. P., I. Wathne, J. Giske, A. Hobæk & P. Larsson. From phantom midges (*Chaoborus flavicans*) to perch (*Perca fluviatilis*): zooplankton community changes (manuscript).

Contents

A. Synthesis

"A fish introduction and its impact on the plankton community"

Introduction

This thesis is about how one species can invade an ecosystem and change the biological community within a few years. Some species disappear and some flourish and others appear that have never been seen before in that habitat. The question is whether such changes could have been expected or were mostly unpredictable?

Since the findings of Hrbacek et al. (1961) and Brooks and Dodson (1965) considerable research has been carried out to describe and predict the effects of predation on zooplankton communities in freshwaters. This is summarized in various reviews and textbooks such as Zaret (1980), Carpenter and Kitchell (1993), Lampert (1993), Brönmark and Hansson (2005), Gliwicz (2003), and Lampert (2011). They all state that size selective predation has a significant effect on the zooplankton community and that changes in the zooplankton cause changes in the phytoplankton through so-called cascading effects where the predation has both direct and indirect effects (Carpenter & Kitchell, 1993).

There is, however, a marked difference between the impact of various kinds of predators, particularly between vertebrate and invertebrate predators. Invertebrate predators are characterized as size-dependent predators. They are not much larger than their prey and are mostly limited to catch and handle only small prey. By becoming big enough, prey can eliminate this risk. Vertebrate predators such as fish are, after only a short period of growth, much larger than their prey and are characterized as gape-limited (Zaret, 1980). They select the largest prey they can gape over and they select large zooplankton, particularly the invertebrate predators. Therefore, in lakes dominated by invertebrate predators, juveniles and small species of zooplankton are most vulnerable to predation, and large zooplankton species will dominate, whereas in lakes with planktivorous fish, the larger individuals suffer from fish predation and small species dominate the zooplankton.

Not all fish feed on zooplankton. Some live on benthic animals and some live on other fish. Most fish start with zooplankton as their first food, but at later ages they switch to larger items and some become piscivorous even in their first year of life.

When a lake has none or few planktivorous fish, it often has a long clear-water phase in the middle of summer (Lampert, 1978). This is caused by large zooplankton species, i.e. waterfleas (*Daphnia* spp.). They are efficient phytoplankton feeders, and they clear up the water containing micro algae. However, these animals are also attractive food for planktivorous fish, and if they are very abundant, the clear water phase is reduced and may be exchanged with an algal bloom.

To improve water quality by biological means, a so-called biomanipulation method has been proposed (Shapiro et al., 1975; Gulati et al., 1990; Kasprzak et al., 2002) to reduce the density of phytoplankton. The principle is very simple: by introducing piscivorous fish to a lake, one will reduce the number of planktivores and by that give the large zooplankton species the possibility to develop and to reduce algal blooms.

Planktivory from fish can also be reduced by other means for instance by directly removing planktivorous fish. Such direct reductions have been made with intense gill net fishing or even by killing all fish with rotenone poisoning (Prejs et al., 1997), but they are rarely completely successful. Therefore, the zooplankton community will only have a short time to adapt to the reduced fish predation.

Periods without fish have sometimes appeared naturally and caused rapid alteration to the zooplankton community. This was found in Lake Mendota in Winsconsin by Vanni et al. (1990) when a complete anoxic hypolimnion caused a mass summer kill of planktivorous fish. However, this event was of short duration and how the plankton community would develop over a longer time period without fish predation is still unclear.

In the present study the situation has been contrary to the case in the biomanipulation experiments mentioned above. We have studied a lake, Lake Myravatn, that for a very long time has been without planktivorous fish (Nilsen, 1980; Knudsen et al., 2006) and where the plankton community was structured to cope with invertebrate predators at pelagic, mainly the larvae of the phantom midge, *Chaoborus flavicans* (Meigen). Recently, most likely in autumn 2006, Eurasian perch, *Perca fluviatilis* (L.) was introduced illegally to the lake and we expected that this would cause large changes. We had a situation where the plankton community was adapted to invertebrate predators, but now it was suddenly facing an efficient planktivorous fish. So in contrast to the situation for many studies, we began with a plankton community of the sort that biomanipulation attempts to create, but due to the illegal perch introduction, the system could switch to the opposite situation one with poorer water quality and a less diverse community. Our challenge was therefore to reveal the effect of fish planktivory on a plankton community that for many years had been without being exposed to planktivorous fish.

1 Background for the present study

According to available records, people began early in the 1800s (Vibe, 1896) to introduce new fish to the lakes and rivers in the Bergen area. Vibe (1896) described where Northern pike, *Esox lucius* (L.) occurred in his time and indicated when the introductions might have taken place and even had names of some of those that carried this out. Lake Myravatn is not specifically mentioned, but nearby lakes got pike about 200 years ago, and it would be reasonable to think that pike were introduced to Lake Myravatn at approximately the same time. The pike eradicated planktivorous fish, mainly brown trout, *Salmo trutta* (L.) and sticklebacks (family: Gasterosteidae) from many small lakes, but no remarkable change was seen in large and deep lakes (Hobæk et al., 2002). In the lakes free of planktivorous fish, zooplankton with adaptive traits towards invertebrate predators increased their density. Lake Myravatn was one such lake, where the larvae of phantom midge (*C. flavicans*) were the dominant pelagic predators and the pelagic zooplankton community was dominated by large filter-feeders, *D. longispina* (Müller) and *D. pulex* (Leydig) (Giske, 1986; Kvam & Kleiven, 1995; Kleiven et al., 1996; Hobæk, 1998; Bjørklund & Brekke, 2001; Jensen et al., 2001; Knudsen et al., 2006). The lake is situated only 31 m above sea level which means that just after the last glaciation it lay close to the sea surface and could be reached by both salmonids and sticklebacks. Its present elevation and waterfall in the outlet brook have arisen in response to the glacial isostatic adjustment. The lake probably originally had a population of three-spined stickleback, *Gasterosteus aculeatus* (L.) that could also be eradicated by the pike. The lake might also have had a trout (*S. trutta* L.) population, but in spite of many studies carried out in the lake, only one single trout has been caught and that was in the outlet brook not in the lake (Jakobsen, pers. comm.). We assume that the pike had consequently predated all trout entering the lake. Since the outlet brook is very short before it ends in a waterfall, and the inlet river enters through a swamp, the conditions for trout recruitment are very poor. So if any trout did occur in the lake they would likely be very insignificant in the biological community. The occurrence of eel, *Anguilla anguilla* (L.) is mentioned in Nilsen (1980), but it has not been caught since, neither by angling nor gill netting. We assume that the population is fairly small.

In 2008 it was discovered that perch (*P. fluviatilis*) had been introduced in Lake Myravatn, and for them the food conditions were excellent and we expected that their appearance would cause marked changes in the food-web. Perch is a generalist feeder (Schleuter & Eckmann, 2008) and feeds on a wide variety of food ontogenetically from small to larger food items up to piscivory and cannibalism (Allen, 1935; Craig, 1974; Persson & Greenberg, 1990; Brabrand, 2001; Byström et al., 2003). It is a widely distributed species in Eurasia from the British Isles in the west to east Siberia in Russia (Craig, 2000). It colonized eastern Norway via the Baltic Sea (when it was freshwater) after the last glaciation (Huitfeldt-Kaas, 1918; Refseth et al., 1998), but it did not reach the western part of the country due to its low salinity adaptation (Linløkken, 2008) and geographic barriers. Over the last two decades, perch has been spread in freshwaters in the Bergen area and the west coast of Norway and this has possibly been done with the intention of increasing pike production for sport fishing. Norwegian law defines such introductions as illegal (Naturmangfoldloven, 2009), but unfortunately there are no records about when, how, and who have spread the perch. Perch introduction was identified first from Grimevatnet (**Figure 1**) in the Bergen area in the early 1990s and it later spread to other lakes in the vicinity, for example to Nesttunvatnet in 1997 and Byrkjelandsvatnet in 2000 (Hobæk, pers. comm.). Although Tveitevatnet and Myravatnet are in the same watershed as Grimevatnet, natural dispersal of the perch was not possible to these lakes because of waterfalls in the rivers originating from these lakes. It was introduced to Lake Myravatn most likely late in 2006 (**Paper I**) and may have also been introduced in the same year or in 2007 to Lake Tveitevatnet (Hobæk, pers. comm.).

Freshwater resources on the west coast of Norway are characterized by low fish predation and simple invertebrate communities because only a few native fish species are present (Hobæk et al., 2002) and they are often dominated by few species, such as the zooplankton community in Lake Myravatn was dominated by large sized daphnids (*D. pulex* and *D. longispina*). Such biologically simple ecosystems are vulnerable to invasion of exotic species viz. fish (Moyle & Light, 1996). Hence, we took the opportunity to study the perch invasion in Lake Myravatn to get an idea of the possible consequences of an invader in this region.

2 Aims of the study

There are published and unpublished data available from Lake Myravatn from the time before the perch appeared that have been used to describe the situation before the introduction (Andreassen, 1977; Nilsen, 1980; Håland, 1983; Giske, 1986; Kvam & Kleiven, 1995; Kleiven et al., 1996; Hobæk, 1998; Bjørklund & Brekke, 2001; Jensen et al., 2001; Knudsen et al., 2006). Unaware of the perch introduction, sampling for a *Chaoborus* study had started in May 2007, almost simultaneously with the first spawning by the introduced perch. This gave us the opportunity to evaluate the perch impact in the initial phase of their introduction. On this basis, the objectives of my intended study were therefore set to:

- Assess how the population of the introduced fish developed and how food preferences change in the developed perch population (**Paper I**).
- Assess the impact of the perch on diel vertical migration (DVM) (**Paper II**) and on the life-cycle and demography of the larvae of *C. flavicans* (**Paper III**).
- Assess the impact of the perch on the zooplankton community (**Paper IV**).

3 Expectations

We expected that the introduction of perch into Lake Myravatn would lead to severe changes in food-web structure. Since the lake had a pH approximately neutral and a dense population of fairly large invertebrates, the water quality and the very good food conditions should allow the introduced fish excellent growth conditions. This would first of all lead to an increased growth of the introduced individuals and thereafter successful reproduction and a rapid population growth of perch. Resident pike were expected to respond to the presence of the new fish prey and slow the development of the perch population. Another aspect was that the dense population would give rise to intraspecific competition and, after a short time, a stunting in the growth and decline in population of the perch.

The plankton community that for centuries had been adapted to mainly invertebrate predators might have lost or reduced their ability to respond adequately to the new predator. They might or might not start to perform diel vertical migration (DVM). This had not been the case before the perch were introduced even though the pike produced kairomones normally producing DVM in the lake and it was difficult to predict whether the plankton would be able to alter their behaviour. Such behaviour is assumed to be beneficial for zooplankton exposed to fish predation, but after 200 years without fish predation would they be able to utilize the dark and oxygen-depleted deeper water layers efficiently? Perch is an efficient plankton feeder and the large daphnids and the *Chaoborus* larvae would be very vulnerable from their predation. Their populations could easily be reduced or they could simply go extinct in the lake and be replaced by other species. Small species like *Bosmina* spp. normally lose out when they compete with larger species, the Daphnids (Gliwicz, 1990), but with a reduction in their competitors they gain an advantage. In lakes with dense perch populations, the plankton normally consists of much smaller cladoceran species than *D. longispina* and *D. pulex,* and it could therefore happen that other smaller species might come to dominate the zooplankton community.

On the basis of these considerations the following expectations were formulated:

- A rapid increase of the perch population due to the good food conditions.
- An individual and numeric response from the pike caused by their predation of perch, reducing the numerical increase of the perch.
- A decimation of the largest zooplankton species due to perch predation
- Change in life-history and behaviour of the largest zooplankton species. The species would start to perform diel vertical migration.
- The abundance and biomass of smaller species would increase.

Study area and methods

1 The study lake

Lake Myravatn (**Figure 1**) is located on the southern outskirts of Bergen City (60° 20' N, 5° 20'E) in the Nesttun watershed on the west coast of Norway at an altitude of 31 m above sea level. It is a small mesotrophic lake (Hobæk & Brettum, unpubl. data) with an average depth of 7.7 m and a surface area of about 59,000 m^2, a volume of about 465,000 m^3 and a maximum depth of 18 m.

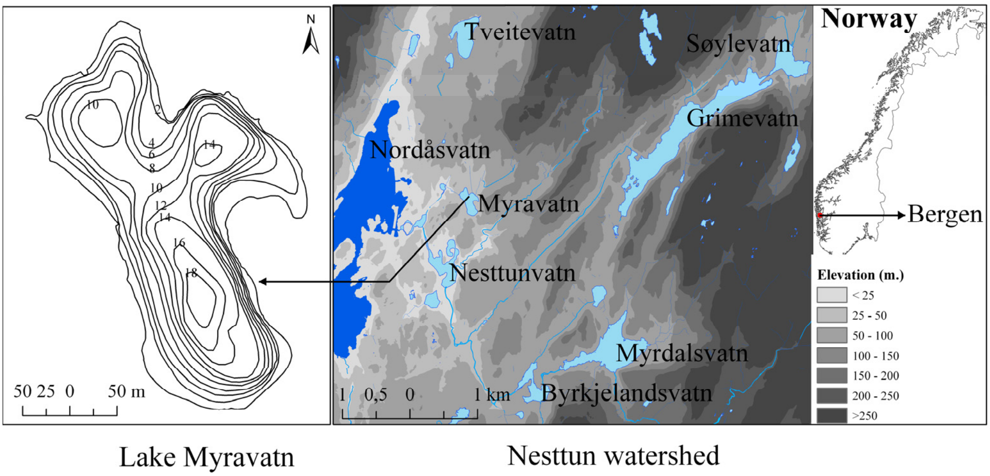

Figure 1 Bathymetric map of Lake Myravatn (left), map of the Nesttun watershed (centre) showing the studied lake, Lake Myravatn and other lakes in the area and part of a North Sea fjord (Nordåsvatn, brackish), and the location of the area (right). The areas of lake and fjord are filled with light blue and dark blue colour respectively.

The lake is normally covered with ice during mid-winter, and thermal stratification occurs during the summer forming an anoxic hypolimnion with a thermocline at about 4-7 m depth. The littoral zone has a 5-10 m macrophyte belt and the inlet river enters the lake through a swamp. The annual mean precipitation is approximately 2000 mm (www.yr.no). Secchi-depth ranges from 1.7 to 4.4 m between mid-spring and mid-autumn and conductivity varies between 50-100 µS cm^{-1}. Chlorophyll *a*, total phosphorus, total organic carbon, and total nitrogen content in the epilimnion vary between >2 up to 20 µg L^{-1}, 22 to 62 µg L^{-1}, >3 to 5.5 mg L^{-1}, and 600 to 1200 µg L^{-1}, respectively (Hobæk, 1998; Bjørklund & Brekke, 2001).

2 Field sampling and laboratory analysis

This part describes briefly the methodological approaches used in this thesis. Details on specific methods are given in the corresponding papers. Fish samples were collected using multi-mesh gill nets (5 m wide x 30 m long) (Nordic survey nets, Appelberg et al., 1995) (**Paper I**). Age and back-calculated size was estimated on the basis of opercula and otoliths (Le Cren, 1947; Nordeng, 1961). Food selection was estimated from stomach analyses (Cortes, 1997). Quantitative samples of zooplankton including the larvae of *C. flavicans* were collected from various depths at the deepest part of the lake using a Schindler trap (Schindler, 1969) (**Papers II, III & IV**). Qualitative samples of zooplankton were collected by hauling a plankton net from near the bottom to the surface. To further document the changes in diel vertical migration and population density of *C. flavicans,* acoustic transect surveys were carried out. Fish gut samples were preserved in 96% alcohol while the zooplankton samples including *C. flavicans* were preserved in 4% sugar formaldehyde (Haney & Hall, 1973) before they were analysed in the laboratory.

Physico-chemical measurements (e.g. water temperature, dissolved oxygen, secchi readings) were carried out on the same day as the zooplankton sampling at the deepest part of the lake.

Results and discussions

1 Development of the perch population

In 2008 we caught three large perch which must have been from those originally released into the lake. It is unknown where they came from but the back calculations based on their opercula showed that they had very poor growth in their original habitat. In their last two years, however, the growth was exceptionally good (**Paper I**). They almost doubled their length in their first year in the lake. On the basis of this we estimated their arrival into Lake Myravatn to be autumn 2006. The catches from autumn 2008 contained lots of 1^+ (1-2 years old) and some 0^+ (<1 year old) perch. It was obvious that the first spawning had taken place in spring 2007 and that reproduction had been very successful. In 2009, the 2007 year-class was much reduced and in numbers approximately equalled the 2008 year-class. These two year-classes dominated in the rest of the study. 0^+ perch were not caught efficiently and therefore it was not possible to estimate the reproduction success from these, but the number of 1^+ perch caught in the subsequent years decreased. This could be due to reduced reproduction, but most likely it was due to increased predation from larger perch and pike (**Paper I**). The individual growth for the youngest age-classes was very high in 2008, but it was reduced thereafter indicating increased competition among the youngest age-classes. Thus, after only two years of spawning, the perch population showed signs of stunting. The population reached an extremely high density in 2008, higher than any found in many lakes investigated in Scandinavia (Heibo & Vøllestad, 2002; Jeppesen et al., 2003).

One of the questions related to the perch introduction into Lake Myravatn was how would the resident pike react to the arrival of a fish prey. Pike is a piscivore, although it might also take ducklings and other vertebrates swimming in the water. In Lake Myravatn it lived mainly on large invertebrates and smaller pike (Nilsen, 1980). We had expected that the pike would respond both in individual growth and numerically in the same way as the perch, but that seemed not to happen. We caught much larger pike than was previously found in the lake (**Paper I**), but the gill-netting which could have revealed any numerical increase, failed to do so. Through the three years we caught altogether five pike. So although the perch already had a potential enemy established in the lake, the pike was unable to hinder the explosive development of the invader. But it may still have had an impact on the behaviour of young perch.

2 Fish predation and zooplankton adaptations

When the perch came, established, and reached its dense population in Lake Myravatn, one of the quickest responses was the adoption of diel vertical migration (DVM) by the largest zooplankton. Before the perch, larger zooplankton species in Lake Myravatn did not show any such behaviour at least by larvae of the *C. flavicans* (**Paper I**). All sizes of *C. flavicans* larvae (I-IV instars) could be found near the surface both day and night, although the mean depth was somewhat deeper for the largest fourth instar than the others. Only the fourth instar larvae showed a weak indication of DVM, but statistically it was insignificant (**Paper II**). After the perch appeared, however, DVM changed for all except the first instar larvae (**Paper II**). The first instar larvae remained in the top water layers both day and night, but the second, third, and fourth instar larvae selected a deeper depth during the day time (**Figure 2**) and by the end of our study period only the first and second instar larvae could be found at shallow depths during the day. Despite the DVM behaviour, the population of *C. flavicans* became very much reduced during the period from 2007 to 2010 (**Paper III**). This was obviously due to fish predation since it was found as one of the main food items in the fish stomachs (**Paper I**). Therefore the DVM they started to perform was not sufficient to avoid decimation of the population. Our interpretation is that although *C. flavicans* lives sympatrically with planktivorous fish in many lakes, the population in Lake Myravatn had been without fish predation for about 200 years, and might have lost some of their DVM abilities. During the 200 years individuals performing DVM would have had no selective advantage, and there must have been a strong selection for individuals not doing DVM. Since there were both pike and eel in the lake, there should be fish kairomones in the water. These chemicals normally induce DVM (Larsson & Dodson, 1993; Tollrian & Harvell, 1999; Laforsch et al., 2006), but since there was no real link between fish kairomones and predation risk, *C. flavicans* may have reduced their sensitivity to fish kairomones as a warning signal. As the effect of fish kairomones has been shown to be density dependent (Loose, 1993), the overwhelmingly dense perch population may have produced so much kairomones that DVM started, but it might not have been enough to avoid visual predators (Aksnes & Utne, 1997). The phantom midges may not have gone deep enough to avoid the perch and so the population became much reduced. Other zooplankton species (*Daphnia* spp.) would have also started to perform DVM after the perch arrived, and details will be published in another PhD thesis by Ingrid Wathne.

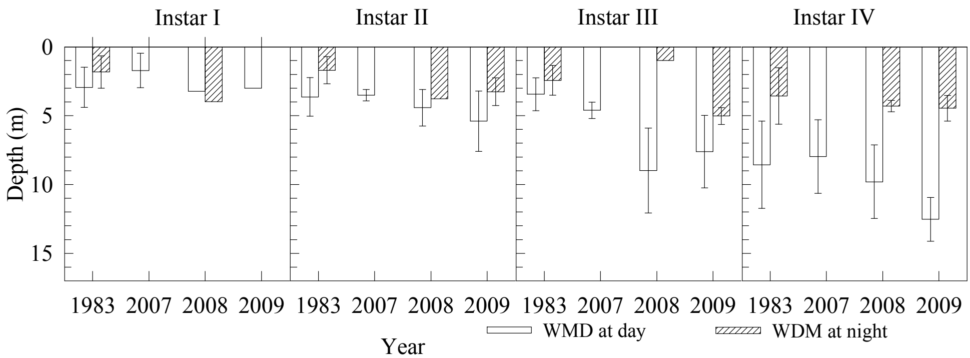

Figure 2 Mean depth (WMD) selected by various instars of *Chaoborus flavicans* during summer (June-September) in various study years. Error bars (standard deviations) are set both sides from mean. Years 1983 and 2007 reflect conditions before the perch introduction and 2008-2009 reflect conditions after the perch introduction.

3 Fish predation and changes in life history

Unpublished data from1983 helped reveal the existence of a rarely known bivoltine life-cycle for *C. flavicans in* Lake Myravatn (**Paper III**). In addition to a generation born in late summer and emerging next May-June, there was also, before the perch arrived, a summer generation of *C. flavicans*. These were born in June and emerged in August. When the perch came, this bivoltine pattern changed to a univoltine life-cycle (**Paper III**). Also the body size of *Chaoborus* larvae became smaller during the period they would normally attain maximum size (April-May). We have interpreted this as a result of extra costs associated with the DVM. In addition to the life-cycle and the body size changes, the population of *Chaoborus* larvae became greatly reduced with the summer population disappearing within four years of the perch introduction. With the larvae performing DVM to prevent predation (**Paper II**), they could only feed during the night and in the day time the largest larvae were hiding in the benthic zone. This zone is colder and would reduce their growth rate (Stich & Lampert, 1984; Dawidowicz & Loose, 1992; Loose & Dawidowicz, 1994). The overwintering larval population started to emerge later in the summer than before and the larvae born in the summer were not able to emerge before the autumn. The winter conditions prevented them from pupating later in the year, and hence, they had to wait for the next spring to be large enough to emerge.

4 Fish predation and zooplankton composition

The zooplankton community changed during the years following the introduction of perch (**Paper IV**). It did not change immediately and it took four years before there appeared dominance of a new species. However, numerical changes took place already in 2008. We found no relationship between any environmental parameters: temperature, oxygen conditions or secchi depth, and found that the main factor altering the zooplankton composition was the introduced perch. This was also reflected in the analyses of the perch stomachs showing that the most attractive food items were the largest invertebrates (**Paper I**). In the pelagic zone these were the daphnids and *C. flavicans* larvae. In 2007, one year after the presumed introduction of perch, the zooplankton composition was almost identical to the composition in 1983 (Giske, 1986; Paper III). This indicated that the zooplankton community could have been stable in periods between 1983 and 2007. The two *Daphnia* species *D. pulex* and *D. longispina* dominated and both *Eudiaptomus gracilis* (Sars) and larvae of *C. flavicans* were very abundant. The reason why the pelagic zooplankton community seemed unaffected by the fish in the first year of their presence, was most likely due to the fact that most of the fish were only small 0^+ and fed in the littoral zone. Another aspect was that the quantity of potential food items was so large the first year that the perch made no significant impact on the prey animals. In 2008, however, the first signs of reduction in the population of *C. flavicans* and *D. pulex* and *D. longispina* were recognized, and this decline continued throughout the study period until the end of 2010. Then all three species had almost become extinct.

Eudiaptomus gracilis is a species that increased in number after the perch invasion. There could be two reasons for this: 1) reduced *Chaoborus* predation allowing higher survival of the nauplii and early copepodite stages and 2) reduced *Daphnia* populations making less competition for phytoplankton and therefore better growth conditions. We believe the last is the most important since it has been shown by others that the nauplii of *Eudiaptomus* are less vulnerable to *Chaoborus* predation than other zooplankton of the same size (Christoffersen, 1990). Also, *Eudiaptomus* is less efficient for nutrient uptake than the large daphnids (Rothhaupt, 1997).

A dramatic change in the zooplankton community occurred in 2010 when *Bosmina longirostris* (Müller) became completely dominant in the pelagic zone. It had often been found near the littoral vegetation previously (Giske, pers. comm.), but it was very rarely found in pelagic zooplankton samples (Giske, 1986). In 2009 it appeared significantly more often, and in 2010 it really flourished. In 2011 it became even more abundant (Wathne, pers. comm.). This species is easy prey for the larvae of *Chaoborus* and not very suitable for fish predation due to its small size. These two factors in addition to their low compatibility towards daphnids made the new situation in Lake Myravatn ideal for them. Reduced predation and reduced competition allowed them to appear at almost 1000 individuals L^{-1} in the pelagic zone in 2010. Also the rotifers species reacted to the changes in the pelagic. More rotifer species became abundant over time but it is difficult to see whether it was due to predation or competition.

The destiny of the various zooplankton species in Lake Myravatn was also reflected in the food selection of the perch (**Paper I**). 1^+ perch were feeding on both zooplankton and benthic animals. The benthic *Asellus aquaticus* (L.) was the main prey in the spring, but during the summer the daphnids and the larvae of *Chaoborus* were the dominant prey. There were many more daphnids than *Chaoborus* so it is difficult to determine which one was most selected, but the stomach analyses verified that they were all exposed to heavy perch predation. Even in 2009 and 2010, when the *Daphnia* spp. populations had been very much reduced, daphnids were still the most abundant prey in the stomachs, indicating a very strong selection for these animals.

Concluding remarks

The conclusion to draw from the present study is that the introduced perch definitely affected the zooplankton composition both directly and indirectly. We found that most of the predictions we made before the study started were verified, which means that the contemporary theoretical understanding of invertebrate and vertebrate predation (Zaret, 1980) gives reasonably good predictions for what will happen when a lake without planktivorous fish and suddenly becomes full of them. The perch flourished after its introduction and the zooplankton changed in behaviour, life history, and numerical presence. The concluding points of this thesis are:

The introduced perch achieved a rapid population increase due to the good food conditions.

- *Chaoborus* changed behaviour by starting diel vertical migration and changed life history from being bivoltine to univoltine.
- The three largest zooplankton species were decimated, almost to extinction.
- Smaller herbivorous species now dominate the pelagic zone.

However there were also unexpected results. The only natural enemy to the perch in the lake, the pike, did not respond quite as expected. Individuals of the species became larger than they previously were, indicating improved food conditions, but the numerical response was weak and they were not able to control the perch population in the first few years after their invasion. The perch took a very short time to establish a very dense population, but it took about three years to alter the zooplankton community. The perch induced diel vertical migration in *Chaoborus*, but the amplitude must have been too small to save them.

Further work

At the end of the present study the lake ecosystem had not stabilized and changes continue to take place. For instance, a new cladoceran species, *Ceriodaphnia quadrangula* (Müller) was discovered and appeared in substantial number in the pelagic zone in 2011 (Wathne, pers. comm.). It has not been observed before. Changes in the macrophyte belt with new underwater species flourishing should be more carefully studied. The development of the pike is also unclear. There is a potentially negative impact on small pike from predation by large perch. Pike is not so easily caught by gill netting and that could have given us a misleading impression of its population density. In the future this species should be followed more directly. We did not study the benthic fauna of the lake and changes among them have most likely taken place. Changes of the previously very common *A. aquaticus* are so far unknown. It occurred very frequently in the perch stomachs and its population may have been significantly reduced, which would also have a negative impact on the pike population. The development of the phytoplankton is something we did not manage to incorporate. This, however, has to be dealt with in future. Thus, to get a complete picture of the impact of the unwanted intruder, there are still many questions to answer.

References

Aksnes, D. L. & A. C. W. Utne, 1997. A revised model of visual range in fish. Sarsia 82: 137-147.

Allen, K., 1935. The food and migration of the perch (*Perca fluviatilis*) in Windermere. Journal of Animal Ecology 4: 264-273.

Andreassen, Ø., 1977. *Asellus aquaticus* (L.) (Crustacea, Isopoda), abundance, migration and life cycle in Lake Myravatn (in Norwegian). MSc. Thesis, University of Bergen, Bergen.

Appelberg, M., H. M. Berger, T. Hesthagen, E. Kleiven, M. Kurkilahti, J. Raitaniemi & M. Rask, 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air and Soil Pollution 85: 401-406.

Bjørklund, A. E. & E. Brekke, 2001. Water quality in Lake Myravatn (in Norwegian). In Overvåking av ferskvannsresipienter i Bergen Kommune i 2000. Haukås-, Nesttun-, Fjøsanger- og Appeltunvassdragene. Rådgivende Biologer As., Bergen 43-74.

Brabrand, A., 2001. Piscivory in larval perch (*Perca fluviatilis*): mechanisms structuring larval roach (*Rutilus rutilus*) cohorts. Ecology of Freshwater Fish 10: 97-104.

Brooks, J. L. & S. I. Dodson, 1965. Predation body size and composition of plankton. Science 150: 28-35.

Brönmark, C. & L. A. Hansson, 2005. The biology of lakes and ponds (2nd edn). Oxford University Press, Oxford.

Byström, P., L. Persson, E. Wahlström & E. Westman, 2003. Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. Journal of Animal Ecology 72: 156-168.

Carpenter, S. R. & J. F. Kitchell (eds), 1993. The trophic cascade in lakes (2nd edition). Cambridge University Press, Cambridge.

Christoffersen, K., 1990. Evaluation of *Chaoborus* predation on natural populations of herbivorous zooplankton in a eutrophic lake. Hydrobiologia 200: 459-466.

Cortes, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54: 726-738.

Craig, J. F., 1974. Population dynamics of perch, *Perca fluviatilis* L. in Slapton Ley, Devon. Freshwater Biology 4: 417-431.

Craig, J. F., 2000. Percid fishes: systematics, ecology and exploitation. Blackwell Science, Dunscore.

Dawidowicz, P. & C. J. Loose, 1992. Metabolic costs during predator-induced diel vertical migration of *Daphnia*. Limnology and Oceanography 37: 1589-1595.

Giske, J., 1986. Factors regulating the populations of two *Daphnia* species in a lake without planktivorous fish (in Norwegian). MSc. Thesis, University of Bergen, Bergen.

Gliwicz, Z. M., 1990. Food thresholds and body size in cladocerans. Nature 343: 638-640.

Gliwicz, Z. M., 2003. Between hazards of starvation and risk of predation: the ecology of offshore animals. International Ecology Institute, Oldendorf/Luhe.

Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer & E. van Donk (eds), 1990. Biomanipulation - tool for water management. Kluwer Academic Publication, Dordrecht/Boston/London.

Haney, J. F. & D. J. Hall, 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. Limnology and Oceanography 23: 331-333.

Heibo, E. & L. A. Vøllestad, 2002. Life-history variation in perch (*Perca fluviatilis* L.) in five neighbouring Norwegian lakes. Ecology of Freshwater Fish 11: 270-280.

Hobæk, A., 1998. Overvåking av ferskvannsresipienter i Bergen Kommune 1997. Gravdals-, Fyllingsdals-, Nesttun- og Appeltunvassdragene (in Norwegian). Norsk Institute for Vannforskning (NIVA), Bergen 83.

Hobæk, A., M. Manca & T. Andersen, 2002. Factors influencing species richness in lacustrine zooplankton. Acta Oecologica 23: 155-163.

Hrbacek, J., M. Dvorakova, V. Korinek & L. Prochazkova, 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie 14: 192-195.

Huitfeldt-Kaas, H., 1918. Ferskvandfiskernes utbredelse og invandring i Norge, med et tillaeg om krebsen. Centraltrykkeriet Kristiania (Oslo).

Håland, A., 1983. Home range use and spacing in Mallard *Anas platyrhynchos* broods. Ornis Scandinavica 14: 24-35.

Jensen, K. H., P. Larsson & G. Hogstedt, 2001. Detecting food search in *Daphnia* in the field. Limnology and Oceanography 46: 1013-1020.

Jeppesen, E., J. P. Jensen, C. Jensen, B. Faafeng, D. O. Hessen, M. Søndergaard, T. Lauridsen, P. Brettum & K. Christoffersen, 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the Temperate Zone to the Arctic. Ecosystems 6: 313-325.

Kasprzak, P., J. Benndorf, T. Mehner & R. Koschel, 2002. Biomanipulation of lake ecosystems: an introduction. Freshwater Biology 47: 2277-2281.

Kleiven, O. T., P. Larsson & A. Hobæk, 1996. Direct distributional response in *Daphnia pulex* to a predator kairomone. Journal of Plankton Research 18: 1341-1348.

Knudsen, F. R., P. Larsson & P. J. Jakobsen, 2006. Acoustic scattering from a larval insect (*Chaoborus flavicans*) at six echosounder frequencies: implication for acoustic estimates of fish abundance. Fisheries Research 79: 84-89.

Kvam, O. V. & O. T. Kleiven, 1995. Diel horizontal migration and swarm formation in *Daphnia* in response to *Chaoborus*. Hydrobiologia 307: 177-184.

Laforsch, C., L. Beccara & R. Tollrian, 2006. Inducible defenses: the relevance of chemical alarm cues in *Daphnia*. Limnology and Oceanography 51: 1466-1472.

Lampert, W., Year. of Publication. Climatic conditions and planktonic interactions as factors controlling the regular succession of spring algal bloom and extremely clear water in Lake Constance. In Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, Denmark, 1977, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart 20: 969-974.

Lampert, W., 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. Archiv für Hydrobiologie Beiheft/Ergebnisse der Limnologie 39: 79-88.

Lampert, W., 2011. *Daphnia*: development of a model organism in ecology and evolution. International Ecology Institute, Luhe.

Larsson, P. & S. Dodson, 1993. Invited review: chemical communication in planktonic animals. Archiv fur Hydrobiologie 129: 129-155.

Le Cren, E. D., 1947. The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. Journal of Animal Ecology 16: 188-204.

Linløkken, A. N., 2008. Population ecology of perch (*Perca fluviatilis*) in boreal lakes. PhD Thesis, Karlstad University, Karlstad.

Loose, C. J., 1993. *Daphnia* diel vertical migration behavior: response to vertebrate predator abundance. Ergebnisse der Limnologie 39: 29-29.

Loose, C. J. & P. Dawidowicz, 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. Ecology 75: 2255-2263.

Moyle, P. B. & T. Light, 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation 78: 149-161.

Naturmangfoldloven, 2009. Lov om forvaltning av naturens mangfold (naturmangfoldloven), 7. Accessed from http://www.lovdata.no/cgi-wift/ldles?doc=/all/nl-20090619-100.html#31 on 26 May 2011.

Nilsen, M., 1980. Gjedda (*Esox lucius* L.) i Myravatn. Population, ernæring og reproduksjon (in Norwegian). MSc. Thesis, University of Bergen, Bergen.

Nordeng, H., 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, North Norway. I. Age and spawning frequency determined from scales and otoliths. Nytt Magazine Zoology 10: 67-123.

Persson, L. & L. A. Greenberg, 1990. Interspecific and intraspecific size class competition affecting resource use and growth of perch (*Perca fluviatilis*). Oikos 59: 97-106.

Prejs, A., J. Pijanowska, P. Koperski, A. Martyniak, S. Boroń & P. Hliwa, 1997. Food-web manipulation in a small, eutrophic Lake Wirbel, Poland: long-term changes in fish biomass and basic measures of water quality. A case study. Hydrobiologia 342-343: 383-386.

Refseth, U. H., C. L. Nesbo, J. E. Stacy, L. A. Vollestad, E. Fjeld & K. S. Jakobsen, 1998. Genetic evidence for different migration routes of freshwater fish into Norway revealed by analysis of current perch (*Perca fluviatilis*) populations in Scandinavia. Molecular Ecology 7: 1015-1027.

Rothhaupt, K. O., 1997. Grazing and nutrient influences of *Daphnia* and *Eudiaptomus* on phytoplankton in laboratory microcosms. Journal of Plankton Research 19: 125-139.

Schindler, D. W., 1969. Two useful devices for vertical plankton and water sampling. Journal of the Fisheries Research Board of Canada 26: 1948-1955.

Schleuter, D. & R. Eckmann, 2008. Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. Ecology of Freshwater Fish 17: 86-99.

Shapiro, J., V. A. Lamarra & M. Lynch, 1975. Biomanipulation: an ecosystem approach to lake restoration. In Brezonik, L. & J. L. Fox (eds), Water quality management through biological control. University of Florida, Gainesville 85-96.

Stich, H. B. & W. Lampert, 1984. Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. Oecologia 61: 192-196.

Tollrian, R. & C. D. Harvell (eds), 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton.

Vanni, M., C. Luecke, J. Kitchell & J. Magnuson, 1990. Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin: implications for biomanipulation. Hydrobiologia 200-201: 329-336.

Vibe, J., 1896. Norges land og folk. Topografisk-historisk-statistisk beskrivelse. Olaf Norli, Kristiania.

Zaret, T. M., 1980. Predation and freshwater communities. Yale University Press, New Haven and London.

B. Individual papers

Errata for
A fish introduction and its impact on the plankton community

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Thesis for the degree philosophiae doctor (PhD)

at the University of Bergen

Bishnu Pd. Regmi

August 2012

Errata (page, para, line)

Format : topic, page, line no/figure no /table no: “original text” – changed to – “new text”

Synthesis, Page 12, line 6: “benthic” – changed to – “bottom”

Paper I, page 14, line 8 in sub-heading: “the introduced fish” – changed to – “fish”.
Paper I, page 14, line 9: “August 2008” – changed to – “2008”.
Paper I, page 24, line 2: “31” – changed to – “94”.
Paper I, page 29, line 3: “13 cm” – changed to – “18 cm”.

Paper II, page 12, line 22: “in summer” – changed to – “(monthly average)”.

Paper III, page 12, line 4: “upper” – changed to – “dark”.
Paper III, page 15, line 8: “2007-2009” – changed to – “2007-2010”.

Paper IV, Page 9, line 20 & 21: “*E*”– changed to –“*J*”.
Paper IV, Page 12, line 13: “much” – changed to – “much reduced”.
Paper IV, Fig. 7: “The four figure plates from top to bottom belong to 2007, 2008, 2009 and 2010” respectively.
Paper IV, Page 18, line 25: “Its (*Chaoborus*)” – changed to – “Its (*E. gracilis*)”.